



The Development of Episodic Memory across the Lifespan: Integrating Behavioral and Neural Evidence

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Episodic memory (EM) refers to the conscious remembering of events and situations relating the past, present, and future (e.g., Tulving, 2002). Researchers in the fields of cognitive child development and cognitive aging have been working on understanding how EM develops and changes within confined age periods. However, remarkably little effort has been invested into comparing the mechanisms that underlie memory changes in childhood and old age. As we show in this article, a lifespan perspective on EM helps to delineate the differences, commonalities, and dependencies among mechanisms that regulate memory functions and development (cf. Craik & Bialystok, 2006).

Lifespan Differences in Memory Plasticity

EM performance increases during childhood and adolescence and declines during old age (e.g., Li et al., 2004). It is important to note that this inverse-U shaped relation between memory performance and age tells us little about its robustness against variations in developmental context. Hence, similar to neuroscientists, lifespan researchers seek to complement descriptive knowledge about average age trends with a systematic exploration of the malleability of these age trends through intervention. In comparison to single-shot comparative research, this focus on plasticity permits a purified assessment of age-based changes in the psychological function under investigation (Lindenberger & Baltes, 1995).

Brehmer, Li, Mueller, Oertzen, and Lindenberger (2007) directly compared memory plasticity from middle childhood to early old age. The authors used a multiphase training design consisting of baseline assessment, strategy instruction, and strategy practice to compare the plasticity of EM performance in younger children aged 9–10, older children aged 11–12, younger adults aged 20–25, and older adults aged 65–78. The participants learned and practiced the Method of Loci, an imagery-based mnemonic technique, to encode and retrieve words by location cues. Children performed at similar levels as older adults at baseline and after receiving instruction in the strategy (see Panel A of Figure 1). However, children profited considerably more than older adults from subsequent practice, leading to a magnification of age differences between children and older adults over the course of the experiment.

Presumably, the instruction gains observed by Brehmer et al. (2007) indicated individuals' ability to use a new mnemonic strategy to actively organize learning materials, hence reflecting differences in baseline plasticity. Practice gains, on the other hand, reflected individuals' latent potential for optimizing the formation and retrieval of new associations, hence reflecting differences in developmental plasticity. The results of Brehmer et al. (2007) indicate that children in middle childhood and older adults differ little in baseline performance and baseline plasticity, but that children possess greater developmental plasticity in EM performance than older adults.¹

In a follow-up study with the same sample, Brehmer et al. (2008) examined the long-term maintenance of the mnemonic strategy 11 months after the completion of the original training study (see Panel B of Figure 1). They tested maintenance performance in two sessions, the first without and the second with mnemonic reinstruction. Children in both age groups spontaneously showed performance improvements beyond the level they had attained 11 months earlier, and did not gain any further from reinstruction. In contrast, older adults showed decreased performance, and improved reliably from the first to the second retest session. These results suggest that developmental plasticity in middle childhood reflects a powerful alliance between learning and maturation that permitted enhancement of skilled EM performance without the need for reinstruction. The overall pattern of findings suggests that the efficiency of cognitive interventions decreases from childhood to old age, pointing to possible practical implications (cf. Knudsen, Heckman, Cameron, & Shonkoff, 2006).

In sum, under suitable conditions for improvement, the performance patterns of children and older adults diverge (Figure 1), suggesting that the mechanisms that limit performance in old age are at least partially different from those that limit performance in childhood. Together with our colleagues, we have proposed a two-component model of EM development that attempts to provide an initial framework for capturing behavioral and neural differences in EM development in childhood and adulthood (Shing, Werkle-Bergner, Li, & Lindenberger, 2008; Shing et al., 2010; Werkle-Bergner, Mueller, Li, & Lindenberger, 2006). Below, we provide a summary of this framework.

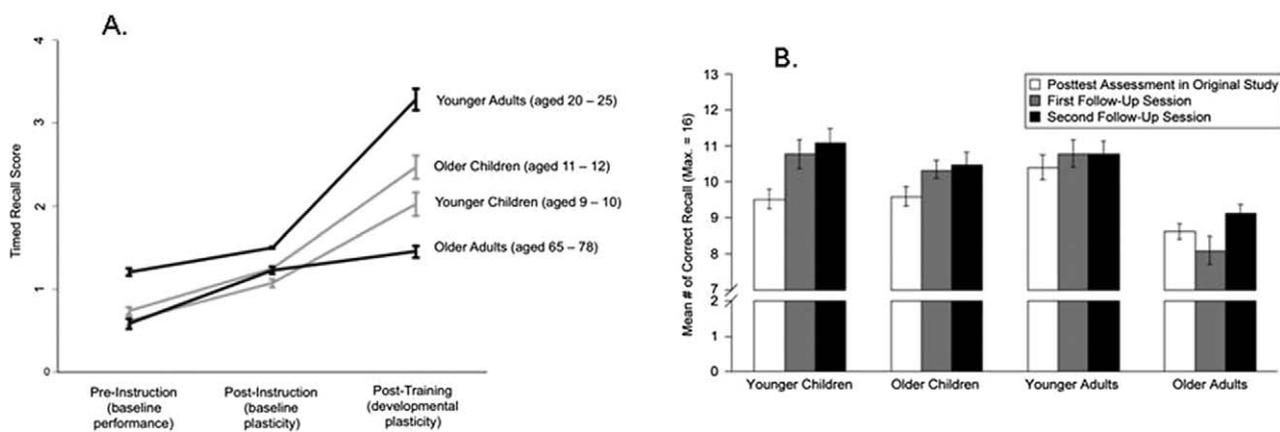


Figure 1. (Panel A) The plasticity of episodic memory is greater in children than in older adults. Memory performance refers to correctly recalled items over encoding time. Post-instruction scores for younger adults cannot be interpreted because of ceiling effects; all other data points can be interpreted. Error bars represent standard errors. Adapted from Brehmer et al. (2007). (Panel B) Average number of correctly recalled words as a function of session and age group. Recall performance is plotted separately for each age group. The white bars represent performance (number of correctly recalled words) in the posttest session of the original study (Brehmer et al., 2007), the gray bars represent performance in the first follow-up session (i.e., without mnemonic reinstruction), and the black bars represent the performance in the second follow-up session (i.e., after reinstruction in the mnemonic technique). Error bars indicate standard errors of the mean. Children (now aged 10–11 and 12–13) improved in skilled episodic memory performance 11 months after training without the need for reinstruction, presumably pointing to a powerful alliance between learning and maturation in middle and late childhood. Older adults showed decreasing trend in their memory performance 11 months after training, but improved further after reinstruction. Adapted from Brehmer et al. (2008).

The Lifespan Dissociation between Strategic and Associative Components of EM

The two-component model of EM development posits two evolving components of EM, one strategic and the other associative, and portrays the ontogeny of EM as the interaction between the two. The *strategic* component refers to cognitive control processes that aid and regulate memory functions at both encoding and retrieval. These processes include elaborating and organizing memory content at encoding, as well as specifying, verifying, monitoring, and evaluating relevant information at retrieval (cf. Simons & Spiers, 2003). The *associative* component refers to binding mechanisms that integrate features of the memory content into coherent representations (Treisman, 1996; Zimmer, Mecklinger, & Lindenberger, 2006). Based on behavioral and neural evidence, the core propositions of the framework are that (1) the associative component of EM matures in middle childhood, and undergoes senescent decline in late adulthood and old age; (2) the strategic component of EM matures later, in approaching adolescence and young adulthood, and undergoes senescent decline in late adulthood and old age. The distinction between strategic and associative components is meant to provide a productive platform for understanding the lifespan development of EM.

To empirically test the developmental predictions emanating from the two-component model, Shing et al. (2008) conducted a lifespan study in which they manipulated the demands on associative and strategic components with a recognition memory task. Participants in the study encoded a list of word pairs. At retrieval, participants received some originally intact pairs, which appeared as pairs at the study phase; some new pairs not studied before; and some rearranged pairs, which included items that were presented at study but paired differently (see Naveh-Benjamin,

2000). Participants were supposed to accept the intact pairs and reject the new and rearranged pairs.

The study manipulated demands on the associative component by using word pairs with (a) low and (b) high associative demand (i.e., German-German “GG” vs. German-Malay “GM” word pairs). At the same time, instructions manipulated the demands on the strategic component by emphasizing (a) incidental item encoding, (b) intentional pair encoding, and (c) elaborative strategic encoding. A practice-based follow-up study for the GM condition sought to induce further improvements in participants’ performance in this condition.

The results are shown in Figure 2. In comparison to children, older adults showed slightly higher initial performance in item- and pair-instruction sessions, presumably reflecting older adults’ ability to make use of their larger repertoire of semantic knowledge to help with encoding new information. At the same time, children showed higher performance gains from strategy instructions for the GG condition and from practice for the GM condition than older adults. Thus, children improved more than older adults in forming associations between memory features when provided with a combination of strategy instruction and task-relevant practice. Older adults’ performance gain was especially low in the high-associative-demand GM condition, supporting the hypothesis that the associative component is impaired among older adults (cf. Old & Naveh-Benjamin, 2008). Age differences in false-alarm rates for rearranged pairs were especially pronounced in the high-associative-demand GM condition, showing older adults’ great difficulties in rejecting rearranged pairs that presumably elicited a strong familiarity response (see also Old & Naveh-Benjamin, 2008). In sum, these data are consistent with a model that posits divergent lifespan trajectories for strategic and associative components of EM.

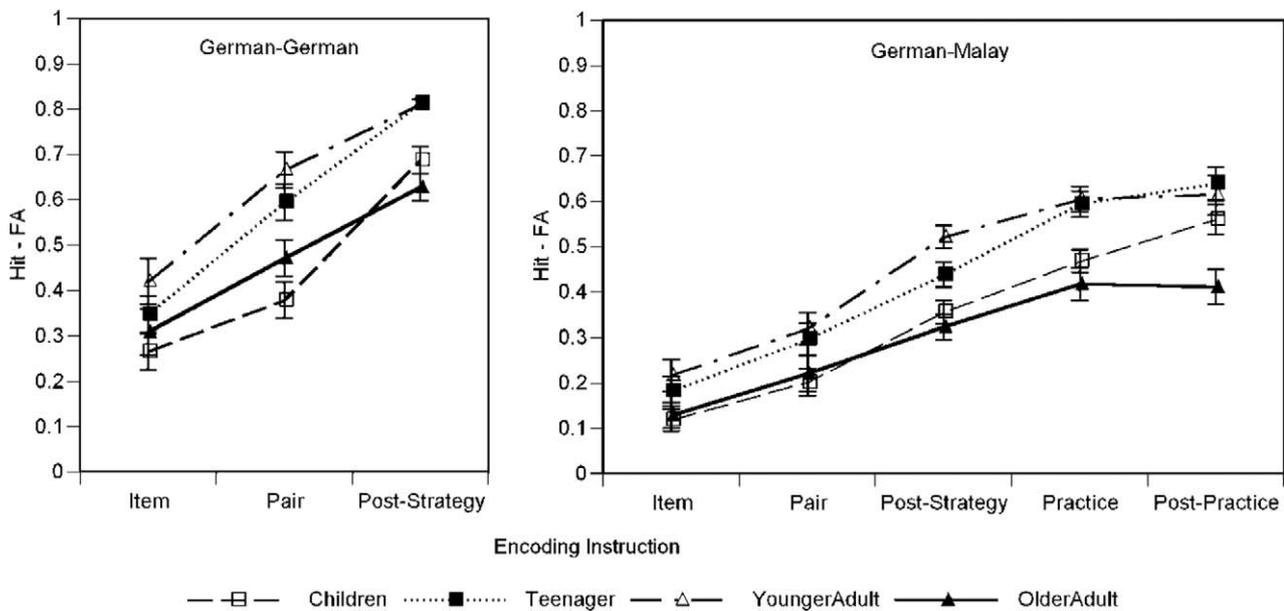


Figure 2. The lifespan dissociation between strategic and associative components of episodic memory. Memory performance refers to correctly recognized pairs (hits) minus erroneously recognized lure pairs (false alarms). Here, the lure pairs consist of words that had been separately presented during encoding. As predicted, children (aged 10–12) overcame their initial strategy deficit through strategic instruction and subsequent practice, and eventually surpassed older adults, demonstrating the efficacy of their associative component. Adapted from Shing et al. (2008).

EM across the Lifespan: Drawing the Neural Picture

Neurocognitive models of EM postulate that the strategic component depends primarily on the prefrontal cortex (PFC), whereas the associative component mostly relies on the medial temporal lobes (MTL), especially the hippocampus (e.g., Simons & Spiers, 2003). The posterior parietal cortex (PPC) is also considered important in more recent conceptions of memory network (e.g., Cabeza, 2008). Anatomical studies show that the PFC, its dorsolateral regions in particular, undergo profound maturational changes well into adolescence (e.g., Gogtay et al., 2004, 2006; Sowell et al., 2003). With respect to brain aging, prefrontal regions show linear declines in cortical volume beginning in the mid-20s (e.g., Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010). The MTL, on the other hand, mature at a relatively faster rate than the PFC, with some evidence pointing to protracted development of some MTL regions (e.g., Gogtay et al., 2006). At the other end of the lifespan, accelerated patterns of decline are observed in MTL regions, with a marked shrinkage observed in the hippocampus and the entorhinal cortex (Raz et al., 2005; Raz, Rodrigue, Head, Kennedy, & Acker, 2004; see also Shing & Lindenberger, 2011 for age patterns in hippocampal subfields).

These structural changes are paralleled by functional activation changes whose patterns are often less clear. Functional magnetic resonance imaging (fMRI) studies support the hypothesis of a link between the slower development of memory for context and detail and the prolonged maturation of lateral PFC (e.g., Ofen et al., 2007). However, a recent study by Ghetti, DeMaster, Yonelinas, and Bunge (2010) also showed age-related differences in functional selectivity in the anterior hippocampus, which may underlie memory for the associations between item and

contextual details. Furthermore, age-related increases in the activation of the posterior parahippocampal gyrus were observed for scenes with higher but not with lower complexity (Chai, Ofen, Jacobs, & Gabrieli, 2010). These results reflect the heterogeneous factors that contribute to memory development, including the increasingly sophisticated use of strategies and control, likely supported by maturation in the PFC, and the evolution of the ability to form complex representation, likely supported by increasing functional specialization within the MTL.

At the other end of the lifespan, age-associated functional impairments in the MTL regions (the hippocampus particularly) have been linked to older adults' difficulties in forming new associations in EM (Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Grady, McIntosh, & Craik, 2003), and in separating new associations from existing memory traces stored in long-term memory (e.g., Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Wilson, Gallagher, Eichenbaum, & Tanila, 2006). Interestingly, the age-related reduction in activity observed in posterior areas of the brain is often coupled with increased bilaterality in frontal activity (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). Increased bilateral activation may indicate a failure to appropriately engage specialized regions, reflecting de-differentiation in processing (Lindenberger & Baltes, 1997; Logan, Sanders, Snyder, Morris, & Buckner, 2002). Alternatively, additional PFC activation in older adults, assumed to indicate additional strategic effort, may reflect attempts to compensate for deficient MTL activation (Cabeza, 2002; Park & Reuter-Lorenz, 2009). The latter interpretation has been challenged by a recent longitudinal study (Nyberg et al., 2010), which revealed longitudinal activity reductions in dorsal frontal cortex, in contrast to cross-sectional analyses suggesting an age-related increase in activation for the same frontal region. The observed discrepancy between

longitudinal and cross-sectional evidence shows that cross-sectional age group differences may not approximate age group changes, underscoring the need for longitudinal investigations of EM development (cf. Nilsson et al., 1997; Schneider, Knopf, & Sodian, 2009).

Future Directions in the Lifespan Study of Episodic Memory

Available behavioral, neuroanatomical, and neurofunctional evidence supports the premise that EM functioning requires the interactive operation of associative and strategic components, and that the two components memory follow different lifespan trajectories, leading to predictable patterns of age-related differences in EM performance. However, the exact nature in which the components of the MTL-PFC network develop throughout the lifespan and how they interact to support memory functioning remains unclear.

A major task for future research will be to comprehensively chart the ontogeny of the two components, testing and refining the guiding propositions of the framework. In particular, there is a clear need to better understand how interactions between the two components are reflected by age-graded changes in the overall EM network. The parietal cortex appears to be particularly important in this context, as it connects PFC and MTL (Cabeza, 2008).

Furthermore, studies motivated by the two-component model of EM development across the lifespan thus far have not included children under the age of eight years (e.g., Brehmer et al., 2007; Shing et al., 2008). Clearly, the model's implications extend into earlier childhood and require further specification. Binding mechanisms, in particular, are fundamentally important for the functioning of EM from early age on (Mitchell & Johnson, 2009), with significant progress around five to six years of age (Sluzenski, Newcombe, & Kovacs, 2006). The neural changes that underlie this behavioral improvement remain to be identified.

Research EM in adulthood and old age also faces difficult challenges. For instance, it remains to be determined (a) whether declines in the strategic component precede declines in the associative component, or vice versa; and (b) whether declines in the associative component are as normative as declines in the strategic component, or foreshadow, to some degree at least, the later onset of dementia (cf. Bäckman, Jones, Berger, Laukka, & Small, 2005; Buckner, 2004).

Lifespan comparisons exacerbate some of the methodological difficulties reflecting the complexities of human development. These challenges range from age-related differences in the physiology of the neuronal and vascular networks (e.g., Harris, Reynell, & Attwell, 2011) to selecting measures that assess the same or equivalent processes across the age ranges under investigation. The productive discussions and helpful recommendations in relation to these issues are encouraging (e.g., D'Esposito, Deouell, & Gazzaley, 2003; Luna, Velanova, & Geier, 2010), and are likely to promote lifespan comparisons.

In sum, the two-component model of EM development portrays the dissociation between associative and strategic aspects of EM across the lifespan. The exact way in which these two components, and the corresponding MTL-PFC

neural network, interact and develop throughout the lifespan remains to be elucidated, and offers exciting venues for future research. Conducting lifespan research poses great methodological challenges, but the conceptual insights emanating from lifespan comparisons are well worth the effort.

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Note

1. For the distinction between baseline performance, baseline plasticity, and developmental plasticity, see Baltes (1987).

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